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TECHNICAL PUBLICATION 88-6

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EFFECTS OF HYDROLOGIC REGIMES ON LIFETIME PRODUCTION AND NUTRIENT DYNAMICS OF CATTAIL

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EFFECTS OF HYDROLOGIC REGIMES ON LIFETIME PRODUCTION AND NUTRIENT DYNAMICS OF CATTAIL

by

Louis A. Toth

(Revised December 1990)

June 1988

Environmental Sciences Division
Resource Planning Department
South Florida Water Management District

Errata Sheet

Pages 9 and 10 of this publication have been revised as follows:

Page 9, paragraph 2:
Line 8: from "approximately 70 %" to "approximately 60 %";
Line 9: from "at least 10 months" to "at least one year";
Line 10: from "60-65 % mortality" to 70-75 % mortality"

Page 10, Figure 5:

From "Survivorship Curves" to "Depletion Curves" and from "ten month Old Plants" to "One-Year" Old Plants.

Revision date: December 1990

EXECUTIVE SUMMARY

Assimilation of surface water nutrients by Everglades plant communities should be an integral component of management strategies for the Water Conservation Areas (WCAs). Nutrient uptake and storage roles of wetlands are well established, but it is not clear if Everglades plant communities permanently remove existing nutrient loads. To evaluate the nutrient storage potential of the WCAs, relationships between hydrologic regimes and nutrient dynamics of existing plant communities need to be established. This study was undertaken to evaluate nutrient dynamics of cattail – a plant species that is replacing sawgrass as the dominant species in some sections of the Everglades.

Lifetime biomass production and associated nutrient uptake are greater where cattail grows in relatively constant, shallow water regimes than in stands subjected to predominantly deep, unnaturally fluctuating water levels. These differences are linked to relationships between hydrologic conditions and nutrient recycling pathways. Because shallow, stable water levels lead to retention of nutrients that are released during plant decomposition, a self-sustaining external recycling pathway develops and provides a continuous supply of nutrients for plant growth. This process tends to maximize plant biomass production and nutrient uptake. In contrast, surface water flow accompanying widely fluctuating water level regimes generally preclude an external recycling pathway and force cattail to rely on internal nutrient storage for new growth and expansion. However, translocation rate constraints limit cattail growth rates and production and make internal recycling ineffective in preventing substantial nutrient export via surface water flow.

Nutrient flux associated with below ground cattail tissues did not appear to be greatly influenced by hydrologic conditions. Due to slow decomposition rates in marsh soils, a proportion of nutrients accumulated by below ground components are probably trapped in the soil complex. Results of this study indicate that below ground plant parts retain and deposit a maximum of 17-19% of total nitrogen and 12-14% of phosphorus accumulated by typical cattail cohorts.

The interaction between hydrologic conditions and nutrient availability appears to mediate cattail expansion in the Water Conservation Areas. Cattail and sawgrass exhibit similar production responses to nutrient regimes associated with shallow, stagnant water conditions; however, due to greater rates of vegetative spreading and annual production (Davis, 1988), cattail has a competitive advantage which may allow it to supplant sawgrass wherever these conditions prevail. In contrast, deep and widely fluctuating water regimes do not appear to be conducive to cattail expansion, even though these conditions have an extremely adverse impact on population characteristics of sawgrass.

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ACKNOWLEDGEMENTS

I would like to first thank Steve Davis, Walt Dineen, and Jim Milleson who provided me with the opportunity to pursue this study. I am also grateful to Steve Guzman and Nancy Urban for their assistance in the field and laboratory. Dan Crean, G. Creighton, B. Martens, B. Nicholas, V. Osmondson, G. Walsh, and staff of the South Florida Water Management District Chemistry Laboratory, particularly M. Rosen and A. Superchi, made invaluable contributions to this study. S. Davis, J.W. Dineen, N. Duplaix, L. Wedderburn, L. Gunderson, D. Haunert, R. Hofstetter, J. Milleson, and D. Worth made helpful comments on an earlier draft of this manuscript.

INTRODUCTION

Multipurpose management objectives have resulted in altered hydrologic and nutrient regimes throughout the Water Conservation Areas (WCA's). Much of the water presently flowing into the system, for example, consists of nutrient-laden runoff from agricultural areas. Although several studies (Gleason et al., 1974; Davis and Harris, 1978; Swift, 1981; Davis, 1982, 1984) suggest that flora and soils of the WCA's quickly assimilate high nutrient loads carried by existing surface water inputs, it is not clear if Everglades plant communities form permanent nutrient sinks. To evaluate the nutrient storage potential of the Water Conservation Areas, it is necessary to establish relationships between nutrient dynamics of Everglades plant communities and hydrologic regimes that result from usage of the WCA's for flood control and water storage.

Nutrient uptake and storage roles of wetlands are well documented (Howell et al., 1974; Tilton et al., 1976; Greeson et al., 1978); however, the effectiveness of wetland plants as nutrient sinks is dependent upon the fate of accumulated nutrients during death and decomposition of plant tissues. Nutrients remaining in dying above ground plant tissues are either translocated and internally recycled (Hopkinson and Schubauer, 1984; Prentki et al., 1978) or returned to surface water during decomposition (Klopatek, 1975; Prentki et al., 1978; Twilley et al., 1977). Nutrients released from decomposing below ground plant components may be assimilated and recycled in new plant growth (Klopatek, 1975; Brinson and Davis, 1976; Prentki et al., 1978; de la Cruz and Hackney, 1977; Gallagher and Plumley, 1979; Barko and Smart, 1980; Hemond, 1983) or permanently stored in the soil complex (Schlesinger, 1978; Dolan et al., 1981). Thus, nutrient storage in below ground plant biomass may be of critical importance when assessing the value of wetland plants as nutrient sinks.

Below ground plant parts form a major portion of the standing crop biomass in many wetland plant communities (Gallagher, 1974; Bristow, 1975; Shaver and Billings, 1975; Brinson and Davis, 1976; de la Cruz and Hackney, 1977; Gallagher and Plumley, 1979). Accumulations of nutrients in below ground plant parts may even exceed nutrient stocks in above ground tissues (Dykyjova and Hradecka, 1976; Dolan et al., 1981); however, nutrient distributions among plant parts commonly undergo periodic flux in association with seasonal growth and/or life history patterns (Klopatek, 1975; Dykyjova and Hradecka, 1976; Prentki et al., 1978; Twilley et al., 1977; Dolan et al., 1981; Gopal and Sharma, 1984). In fact, translocation of nutrients to below ground parts during plant senescence may be an important means by which plants conserve nutrients for use in subsequent new growth (Bayly and O'Neill, 1972; Klopatek, 1975; Twilley et al., 1977; Prentki et al., 1978; Hopkinson and Schubauer, 1984).

Sawgrass (Cladium jamaicense) is the most widespread plant species in the Everglades, and historically covered about 65 to 70 percent of the marsh in monospecific stands or in association with a variety of other macrophyte species (Loveless, 1959). However, as a result of altered hydrologic and/or nutrient regimes, sawgrass is gradually being replaced by cattail (Typha spp.) as the dominant marsh species in some sections of the Water Conservation Areas. Based upon measurements of leaf production at sites exposed to variable surface water nutrient loads, Davis (1984, 1988) has suggested that this change is attributable to cattail's ability to respond to short-term increases in nutrient availability. This study evaluates the nutrient storage potential of cattail through: (1) comparative measurements of production and nutrient accumulation by above ground and below ground plant components; and (2) estimates of nutrient release associated with plant or tissue death. These parameters are evaluated in Everglades habitats with altered hydrologic regimes. Results will be compared with a similar study on sawgrass (Toth, 1987).

PURPOSE AND SCOPE

Much of the original Everglades presently encompassed by the three Water Conservation Areas has been subjected to altered hydrologic and nutrient regimes. Implementation of management options such as backpumping, the Lake Okeechobee Interim Action Plan, and increased usage of the Water Conservation Areas for water storage would exacerbate these environmental modifications. Ongoing studies by Environmental Sciences Division staff are designed to evaluate effects of altered environmental conditions on Everglades plant communities. Much of this work focuses on the ability of wetland flora to remove surface water nutrients, and how environmental conditions, such as hydroperiod and nutrient loads, affect this function. Previous studies have analyzed nutrient flux associated with production and decomposition of above ground plant parts. This study complements these efforts by evaluating effects of water levels on production and nutrient dynamics of below ground components of cattail - a species that is replacing sawgrass as the dominant marsh species in some sections of the Water Conservation Areas. Results will be compared to a similar study on sawgrass to

determine if altered hydrologic regimes are contributing to cattail expansion in the Everglades.

METHODS

Study Area

The study was conducted in Water Conservation Area 2A, Palm Beach and Broward Counties, FL. (Figure 1A). Nutrient enriched water enters this 547 km^2 marsh through three spillways (S-10A, C, and D) in levee L-39, flows south over the marsh, and exits into WCA 2B and 3A via culverts in levee L-35B and spillways (S-11 A, B, C) in levee L-38E (Figure 1B).

Two sampling sites with contrasting hydrologic characteristics were chosen. All sampling at site NLC (north levee cattail) was conducted 10-20 m south of L-39, approximately 1.84 km northwest of structure S-10D. This site was characterized by monospecific cattail (Typha domingensis) marsh, which was typically exposed to shallow surface water levels throughout the year. Site SLC (south levee cattail) was located about 150 m north of levee L-35B and culvert S-145, in a region of WCA 2A that was subjected to predominately deep but widely fluctuating water levels. All sampling at this site was conducted in a T. domingensis stand along the northeast border of a slough opposite S-145.

Plant Sampling

Four cattail samples were taken at each site in February, April, July, and September-October 1984, and January-February 1985. Each sample contained plants representing different life history stages, including both live and dead shoots. Samples were obtained by enclosing a clump of cattail plants within a 87 cm high, 55 cm diameter polyethylene, open-bottom cylinder. To ensure that entire root systems of all enclosed plants were harvested, samples were selected so that plants were not positioned against the inside edge of the cylinder. While digging around its outside periphery with a long-bladed (root-pruning) shovel, the cylinder was gradually pushed into the organic sediment to a depth of about 50 cm. The bottom plane of the enclosed area was cleaved from the soil below, allowing the cylinder and solid core to be lifted *en masse* from the substrate.

All cattail plants within each sample were categorized as live, dead or remnant. All live plants had green leaves, except young new shoots, which had white leaves. Dead plants possessed long (though sometimes broken), light brown dead leaves, while only "remnant" leaves (Figure 2) - the partially decomposed bases of dead leaves - remained on remnant plants. Thus, remnant plants had been dead longer than dead plants and had undergone at least initial stages of decomposition. In fact, some remnant plants were buried within the soil.

Components of each plant were separated as individual plants were extracted from a sample. First, plants were extracted by washing loose soil from the below ground portion of the sample until a cattail shoot base (Figure 2) was exposed. Rhizomes and roots were then detached from the shoot base, carefully separated from soil, and rinsed free of adhering debris. Next, remnant leaves were removed and the shoot base and aerial parts of the plant were separated from the sample. Aboveground plant parts (i.e., live and dead leaves) were then detached from the shoot base and separated. All live, dead, and remnant leaves of live plants were counted. Lengths of intact live leaves were measured to the nearest 1.0 cm and dead portions of these leaves were separated and combined with dead leaves. Lengths of shoot bases were measured to the nearest 0.5 cm. This process was repeated until all plants in the sample were extracted.

Components of each plant were dried for four days at 90° C, weighed to the nearest 0.01 g, ground in a Wiley mill, and analyzed for nitrogen (N) and phosphorus (P) concentrations by the Soil Chemistry Laboratory of the South Florida Water Management District. Due to procedural limitations, plant component samples weighing less than 0.75 g were combined with other comparable samples (e.g., live leaves of two or more new shoots) prior to nutrient analysis. Plant tissue nutrient analyses were performed with Technicon AutoAnalyzer II, after Kjeldahl digestion of N and P using a block digester (modification of Black, 1965).

To compare growth rates of individual plants, shoot bases of subsamples of 50 marked new shoots were measured at monthly intervals until all plants died. Shoot base lengths provide an index of plant growth because cattail shoot bases elongate as new leaves develop at the shoot apex.

Soil Sampling

Two replicate cylindrical soil cores, 7 cm in diameter and 20 cm deep, were taken along the outside periphery of each plant sample (i.e., eight cores/site/sampling period). Soil cores were transported to the laboratory and frozen upright. Frozen cores were cut into 10 cm long sections, dried, ground in a Wiley mill, and analyzed for N and P concentration with the Technicon AutoAnalyzer II (see above).

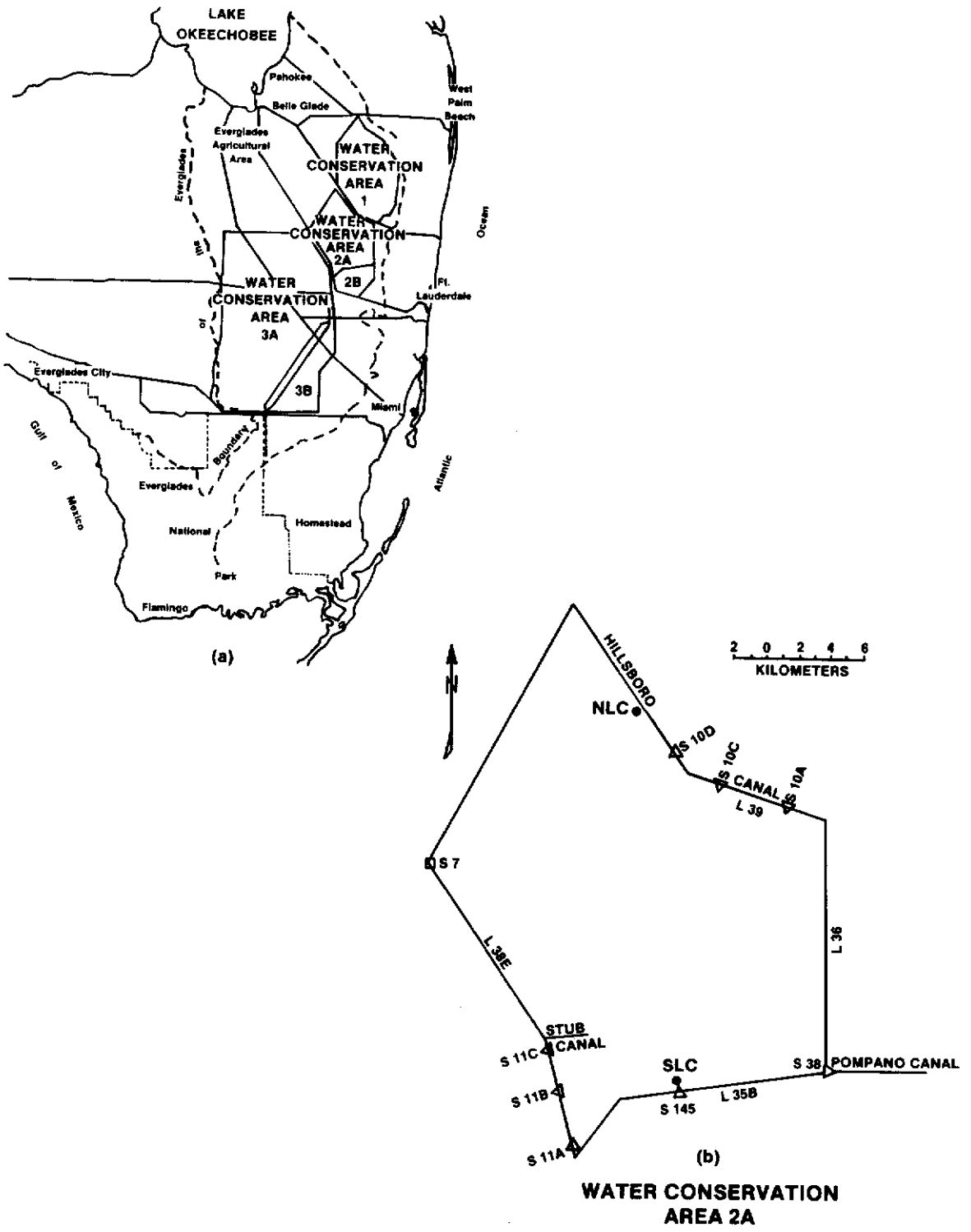

FIGURE 1 Location of Cattail Sampling Sites. (a) Map of South Florida Showing Water Conservation Areas, (b) Water Conservation Area 2A Showing Location of Sample Sites NLC and SLC.

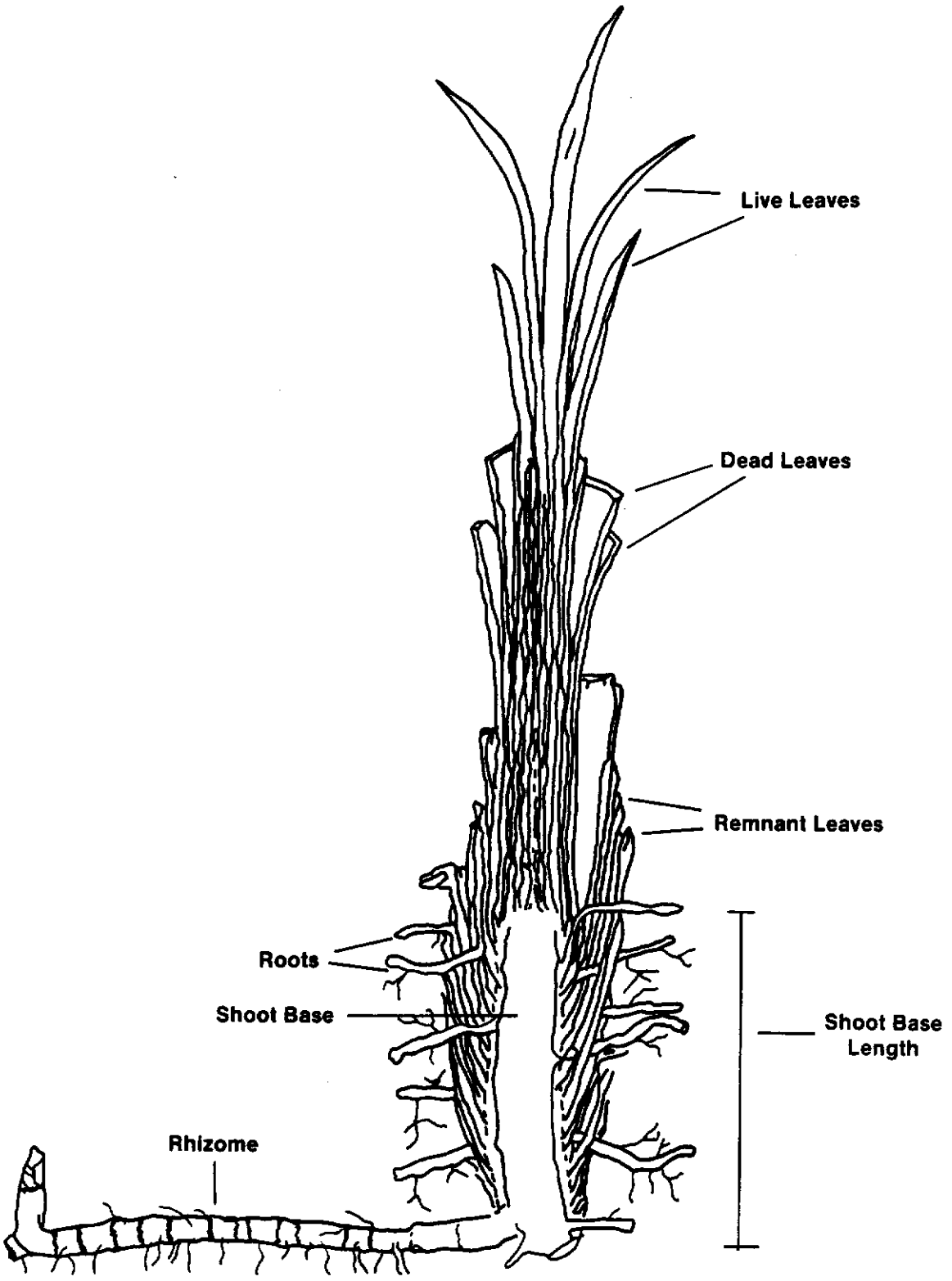

FIGURE 2 Schematic of Cattail Plant.

Water Sampling

Two replicate 1.0 L water samples were collected on each sampling date (i.e., four samples /site/sampling period) and at monthly intervals (or more frequently) during interim periods. Water samples were analyzed (Standard Methods, 1971) for total dissolved phosphorus and nitrogen fractions using a Technicon AutoAnalyzer II by the South Florida Water Management District Water Chemistry Laboratory. Samples for total dissolved phosphorus analyses were digested using an autoclave. Samples for total dissolved nitrogen were digested by the Kjeldahl procedure using a block digester.

Water depths (nearest 0.1 cm), relative to mean ground elevation at each site, were recorded on each sampling date, and at monthly intervals (or more frequently) during interim periods.

Previous analyses of surface water in the sawgrass marsh adjacent SLC and a sawgrass stand 0.75 km west of NLC (see Toth, 1987) provided additional hydrologic and water chemistry data from these regions of WCA 2A.

RESULTS

Surface Water Depths and Nutrient Concentrations

Hydrographs from 1982-1985 (Figure 3A) illustrate differences in surface water depths between the two sampling locations, as well as differential site responses to controlled drawdowns. Water depths at SLC were widely fluctuating and considerably higher than those at NLC during wet season months. Stages at NLC were characteristically stable, rising only briefly during periods of heavy rainfall. During dry season drawdowns, water depths at SLC fell below the soil surface, while shallow surface water levels were generally maintained at NLC by ground water seepage from WCA 1 (i.e., beneath the L-39 levee, Figure 1).

Ambient surface water nutrient concentrations were not consistently different at NLC and SLC (Figure 3) and neither site was subjected to nutrient "enrichment" typical of areas influenced by agricultural surface water runoff (Davis, 1984). However, sharp increases in dissolved nitrogen and phosphorus fractions were recorded when water levels approached ground elevations at each site. Elevated nitrate (NO_3) concentrations (Figure 3D), for example, were detected at SLC from January-April 1984 while dissolved organic phosphorus (Figure 3G), ortho-phosphate (OPO_4) (Figure 3F), and ammonia (NH_4) (Figure 3C) spikes were found at NLC during September 1984. Short-term increases in dissolved nitrogen and phosphorus fractions typically occur in Everglades marshes during falling water levels (Swift and Nicholas, 1986), and are likely due to release of ions during decomposition of organic matter.

Soil Nutrient Concentrations

Significant differences (two-way ANOVA: $p(F) < 0.05$) in soil nitrogen (TKN) and phosphorus concentrations were detected among sampling dates as well as between soil depths and sampling sites (Table 1). Differences in soil nitrogen and phosphorus concentrations among sampling dates did not display any distinct seasonal pattern or appear to be correlated with changes in surface water depths or nutrient concentrations. Nitrogen concentrations were significantly higher in the surface (i.e., 0-10 cm) soil layer at SLC, but did not vary significantly with depth at NLC. Phosphorus concentrations declined with depth at both sites. Site comparisons show that phosphorus concentrations in surface soil samples and nitrogen concentrations in the subsurface (10-20 cm) soil layer were consistently higher at NLC than at SLC. However, nitrogen concentrations in surface soil samples were higher at SLC than at NLC during four of the five sampling dates.

Stand Characteristics

The structure and content of cattail samples revealed subtle differences in plant growth characteristics at the two sites. At NLC, new shoots emerged as deep as 50 cm below ground, in a "soupy", loosely consolidated soil consisting of saturated, decomposing plant material. At SLC, where water levels periodically drop below ground, soils are more compact and cattails develop just below the soil surface. Other site characteristics, such as the presence of willow (Salix) stumps at NLC and remnant sawgrass (Cladium jamaicense) tussocks at SLC, indicate that both stands are of an "invasive" nature. While cattail invasion at SLC appears to have occurred recently and is proceeding with encroachment into open areas of the sawgrass marsh as well as sections of the adjacent slough, the cattail stand at NLC is dense and dominates the former willow zone south of the L-39 levee.

Cattail growth rates also appeared to differ at NLC and SLC. Since the rate at which shoot bases elongate as new leaves are produced (i.e., slopes of linear regressions in Figure 4) is similar at NLC and SLC (ANCOVA, $p(F) > 0.20$), comparable increases in shoot base length reflect equivalent increments of plant growth at these sites. After nine months of

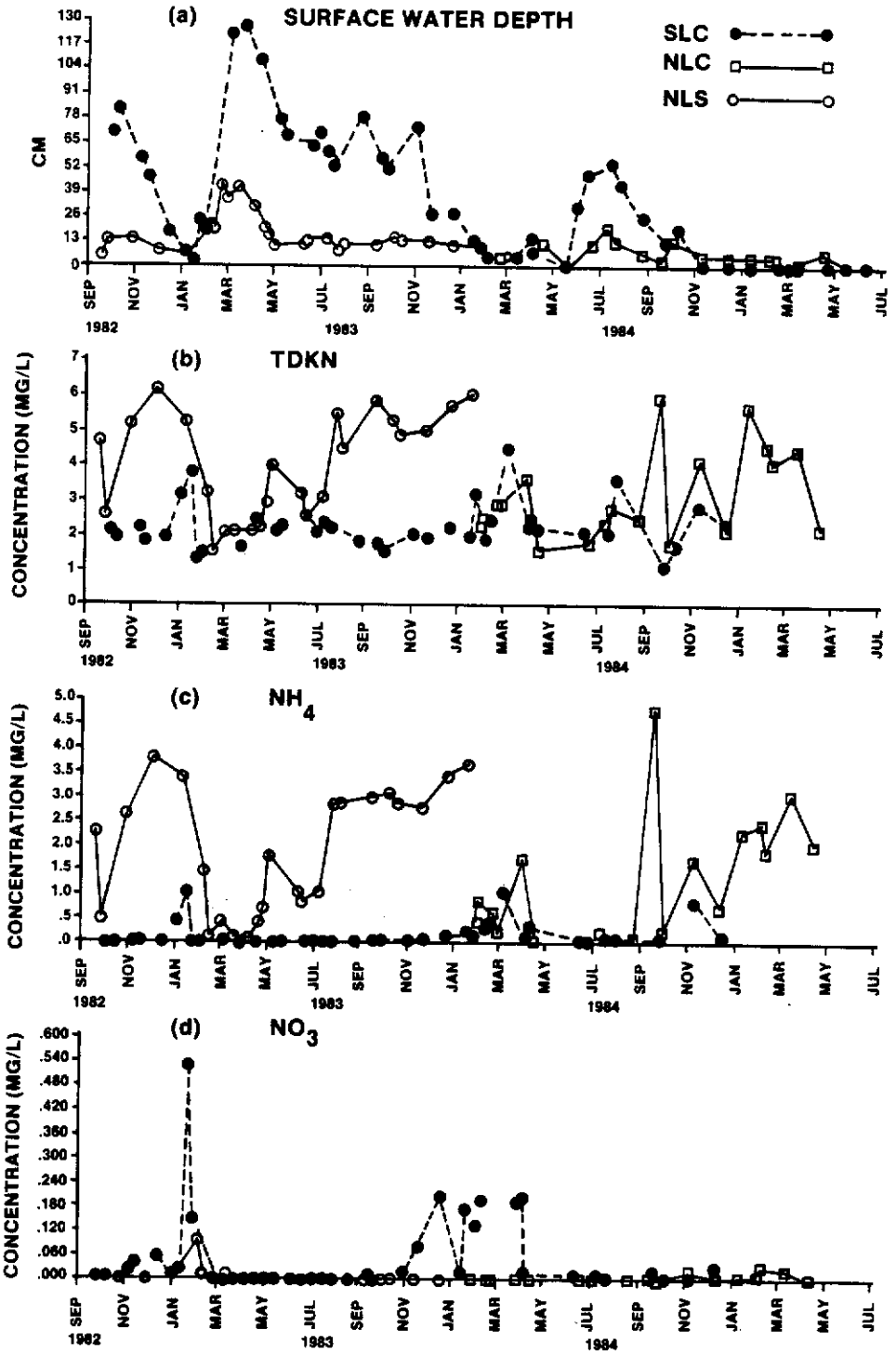

FIGURE 3 Surface Water Depths and Nutrient Concentrations at NLC and SLC (September 1982 - January 1984). Earlier Data Collected at a Sawgrass Stand (Site NLS) 0.75 km West of NLC is also Shown. (a) Depth, (b) Total Dissolved Kjeldahl Nitrogen, (c) Ammonia, (d) Nitrate,

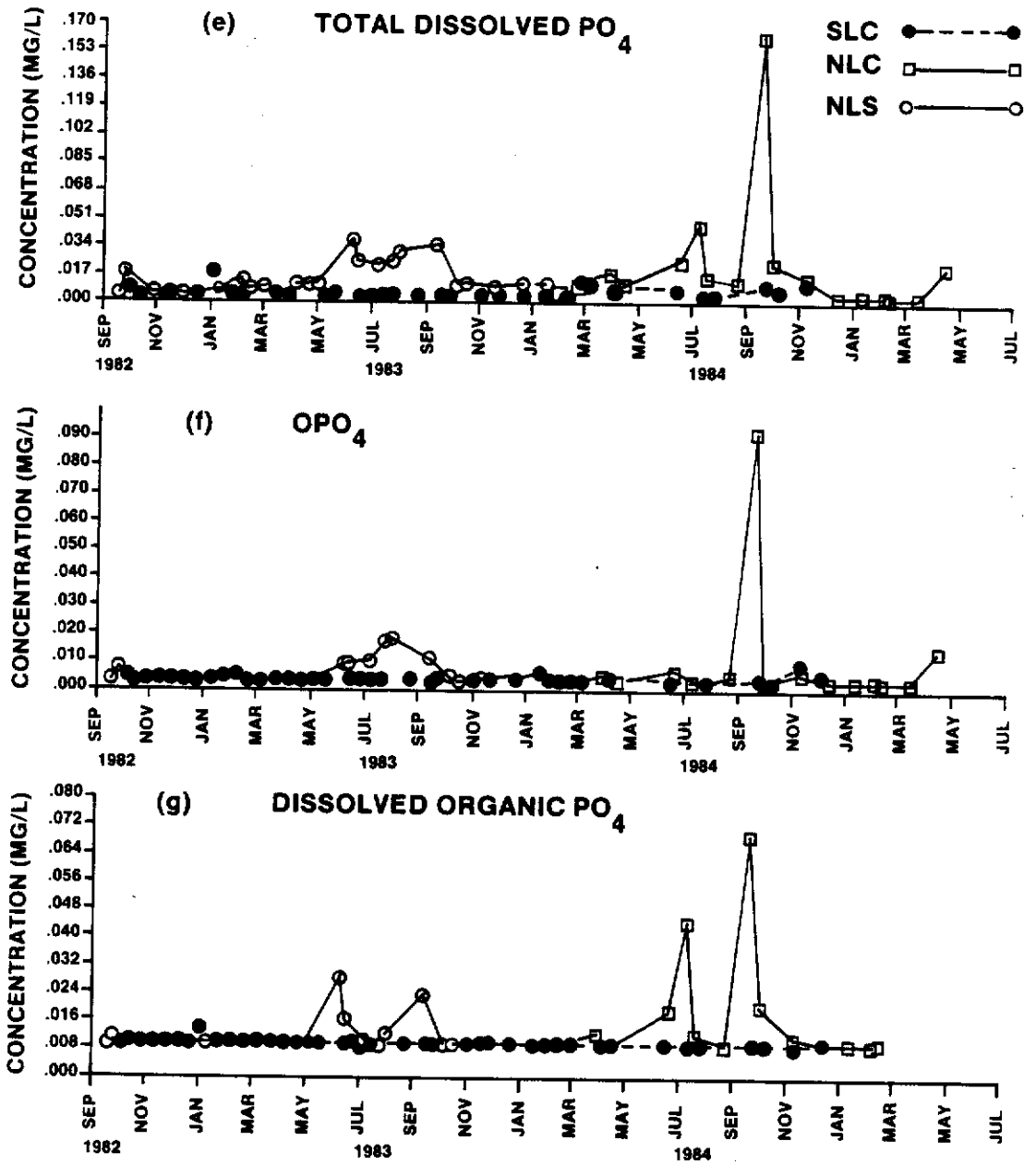

FIGURE 3 Continued (e) Total Dissolved Phosphate, (f) Dissolved Organic Phosphate, (g) Orthophosphate.

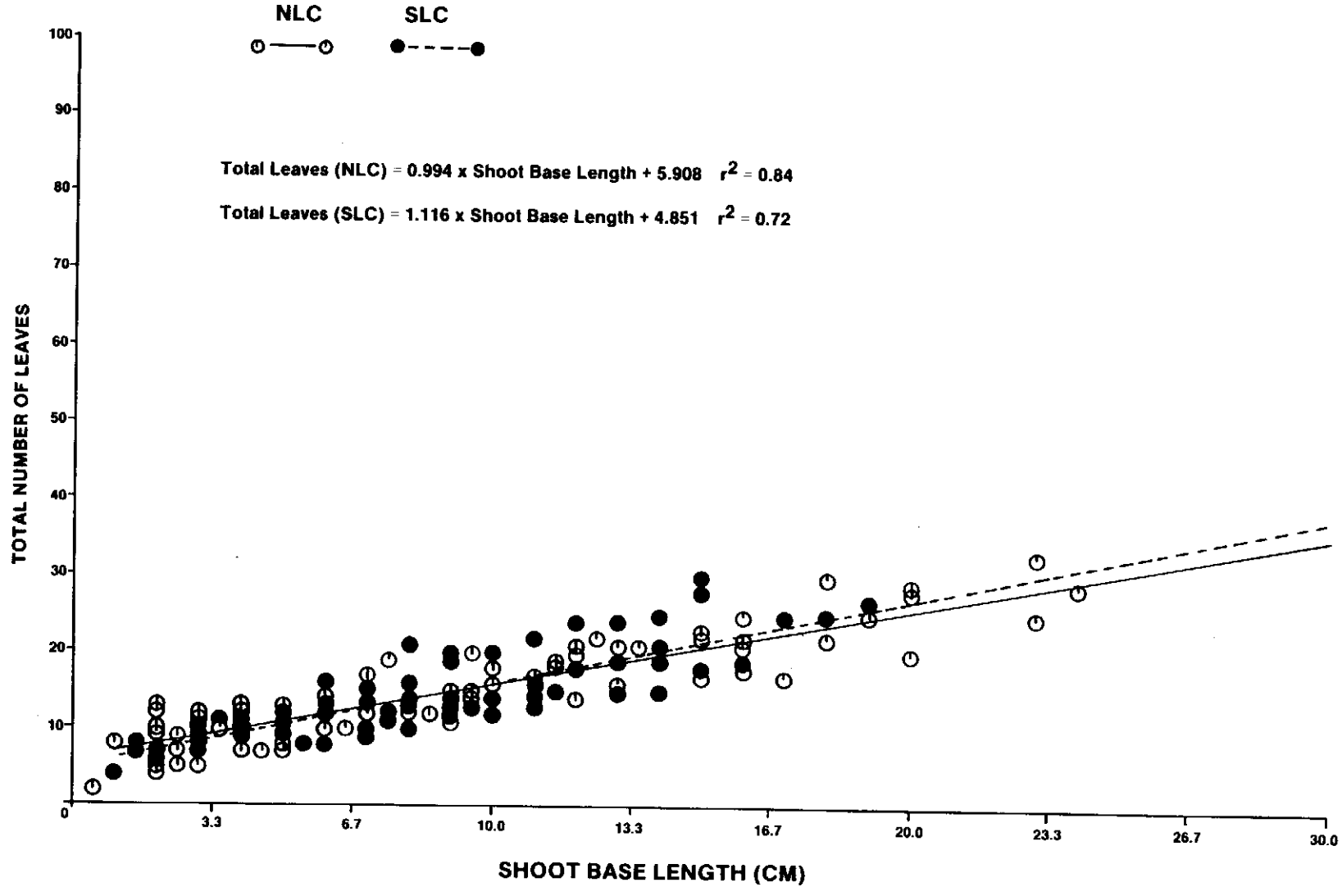

FIGURE 4 Relationships Between Shoot Base Lengths and the Total Number of Leaves Produced by Harvested Live Plants at NLC and SLC.

TABLE 1. Mean Nitrogen and Phosphorus Concentrations (% Dry Weight) of Soil Samples. (Except as noted, all "main effect" factors were significant ($p(F) < 0.05$) and all interaction terms were non-significant ($p(F) < 0.05$.)

Site	Depth (cm)	Winter 1984	Spring 1984	Summer 1984	Fall 1984	Winter 1985
			NITROGEN			
NLC+	0-10++	2.24	2.88	2.52	2.74	2.94
	10-20*	2.73	2.67	2.99	3.03	2.93
SLC	0-10++	2.81	3.03	2.81	3.02	2.55
	10-20*	2.70	2.57	2.71	2.73	2.54
			PHOSPHORUS			
NLC	0-10	0.075	0.038	0.059	0.069	0.050
	10-20++	0.043	0.013	0.031	0.025	0.015
SLC	0-10	0.045	0.031	0.030	0.036	0.048
	10-20++	0.025	0.010	0.025	0.009	0.037

+ Date and depth factors not significant in Date X Depth ANOVA of NLC soils.
++ Significant interaction terms in Date X Site ANOVA's of nitrogen concentrationsof 0-10 cm soil layer and phosphorus concentrations of 10-20 cm soil layer.
*Date factor not significant in Date X Site ANOVA of 10-20 cm soil layer.

growth, shoot base lengths of marked new shoots at NLC measured an average of 11.6 $\pm$ 1.0 (S.E.) cm, while mean shoot base lengths of marked shoots at SLC were only 8.3 $\pm$ 0.4 cm long after 10 months of growth. Thus, plant growth rates were slower at SLC.

Depletion curves (Figure 5) were generated from frequency distributions of shoot base lengths from harvested dead and remnant plants. This methodology is similar to Kreb's (1972) illustrations of life table derivation based upon collections of Dall mountain sheep skulls. Based upon age and growth relationships of marked plants, these curves indicate that approximately 60% of new cattail shoots at SLC survive at least one year, while plants at NLC suffer 70-75% mortality during this period. However, due to faster growth rates at NLC, survival rates of advanced growth stages (i.e., plants with shoot base lengths > 10 cm) were higher at this site than at SLC.

Production

Using shoot base length as an index of plant growth, estimates of cumulative (lifetime) leaf production were derived from leaf growth functions and leaf length-weight regressions. The basis of these estimates was provided by high correlations between shoot base length and the number of leaves produced during a plant's lifetime (Figure 4). These linear relationships were not significantly different between NLC and SLC (ANCOVA: $p(F) > 0.20$). In contrast, asymptotic relationships between live leaf lengths and shoot base length (Figure 6 and Table 2) indicated that leaves of cattails grew taller at NLC, while adjusted means of leaf length-weight regressions were significantly higher at SLC (Figure 7). Integration of these relationships results in the following model of cumulative leaf production (CLP) in relation to plant growth:

TABLE 2. Mean Maximum Live Leaf Lengths (cm) of Cattail Growth Stages at NLC and SLC.

Shoot Base Length (cm)	NLC	SLC
0.5 - 1.0	14.7	10.0
1.5 - 2.0	77.9	17.3
2.5 - 3.0	117.6	78.4
3.5 - 4.0	190.2	179.7
4.5 - 5.0	222.1	178.9
5.5 - 6.0	283.2	214.6
> 6.0	320.2	307.1

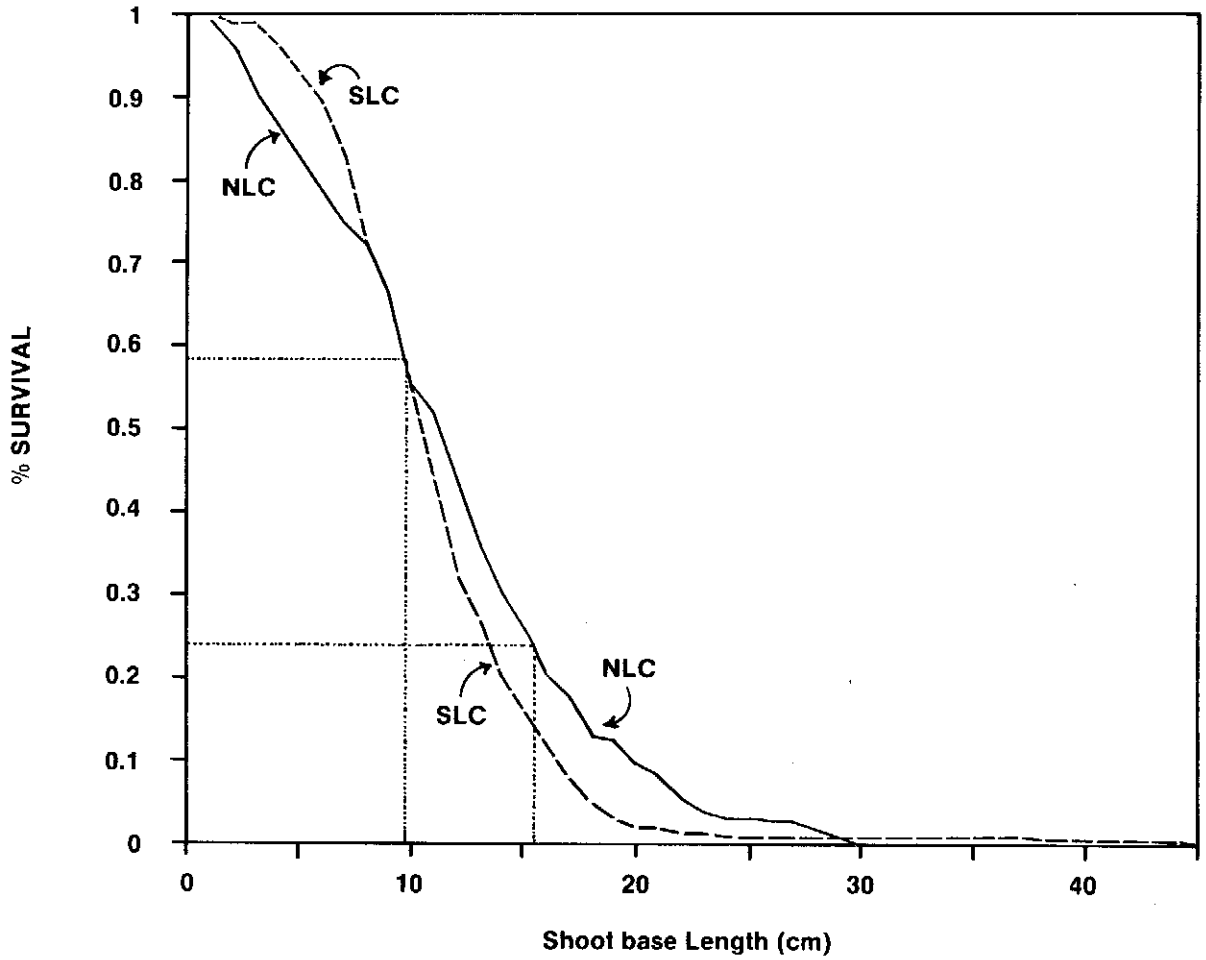

FIGURE 5 Depletion Curves for Typical Cattail Cohorts at NLC and SLC Dotted Lines Indicate Percent Survival and Mean Shoot Base Lengths of One Year Old Plants at Each Site.

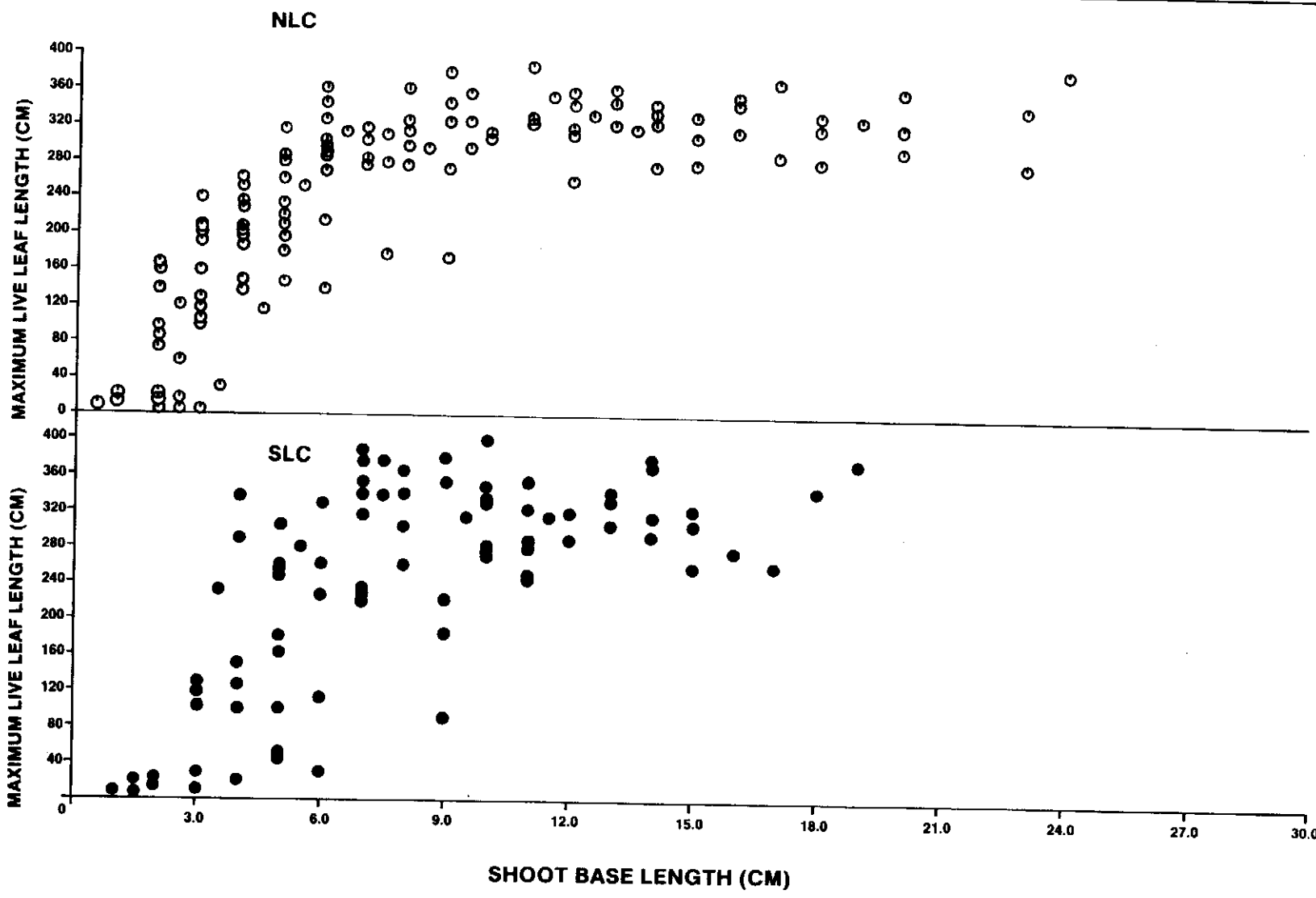

FIGURE 6 Maximum Live Leaf Lengths in Relation to Shoot Base Lengths of Harvested Plants at NLC and SLC.

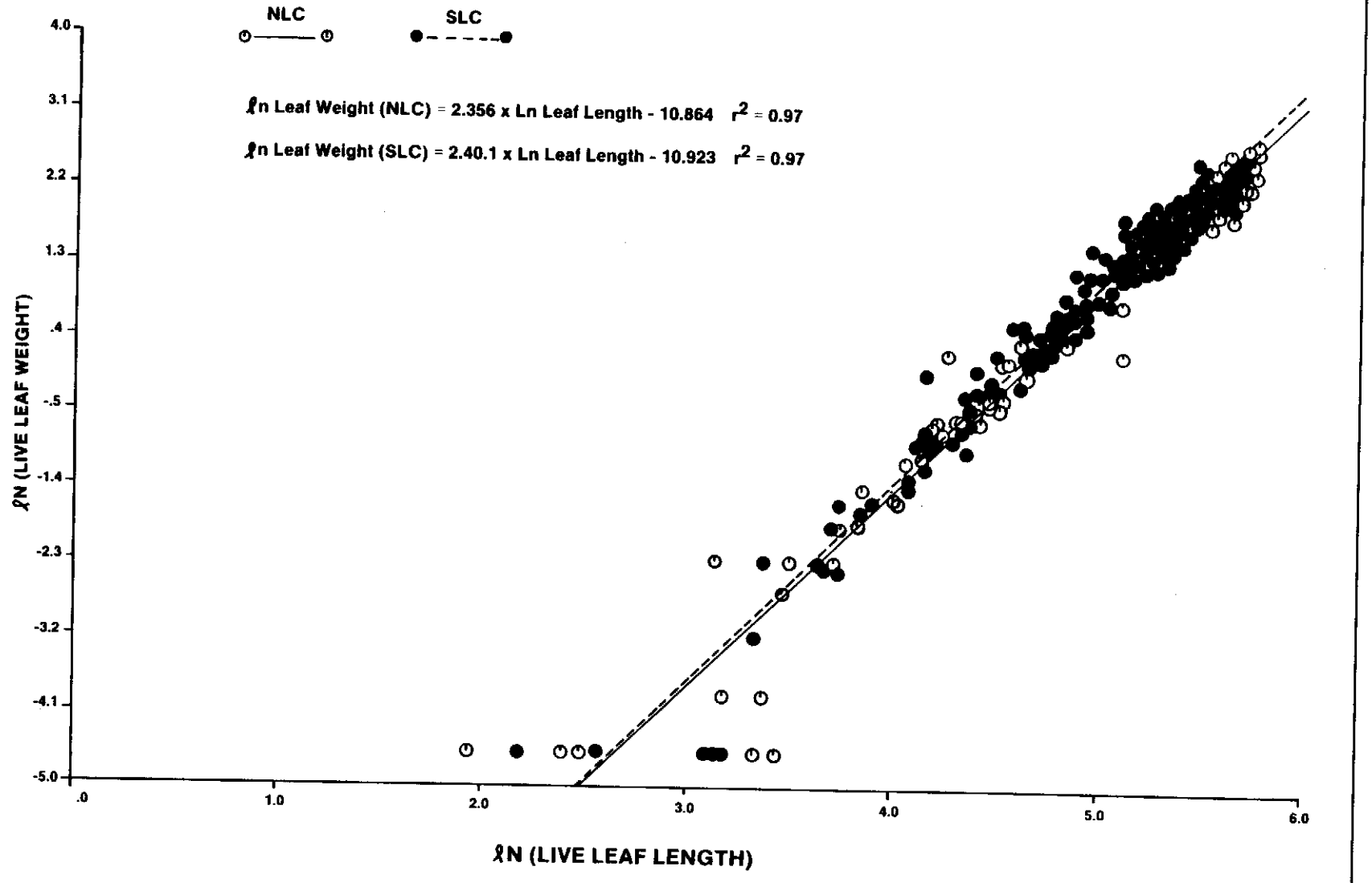

FIGURE 7 Log_e - Log_e Relationships Between Live Leaf Lengths and Weights at NLC and SLC.

$$CLP(s) = \sum_{i=1.0}^{x} Y(i) * (MLW (YMAX(i)) \quad (1)$$

where

x = shoot base length
s = site
Y(i) = number of leaves produced by individual plants at site (s) during the interval in which shoot base lengths increased from i - 1.0 to i (based on linear regressions shown in Figure 4).
YMAX(i) = mean maximum live leaf length of plants at site (s) with shoot base lengths = i when $i \leq 6.0$. Mean maximum live leaf length of all plants at site (s) with shoot base lengths > 6.0 was used when i > 6.0. (see Table 2).
MLW(i) = computed weight of YMAX(i) (based on regressions shown in Figure 7).

Estimates of cumulative leaf biomass production of advanced growth stages (i.e., plants with shoot base lengths >10 cm) were higher for cattail at SLC than NLC (Figure 8A); however, cohort leaf biomass production, calculated as

$$CHLP_{(s)} = \sum_{i=1.0}^{x} S(i) * CLP(i) \quad (2)$$

where

x = shoot base length
s = site
S(i) = site specific survivorship of cattail with shoot base lengths = i (see Figure 5)
CLP(i) = site specific cumulative leaf production of cattail with shoot base lengths = i (based on equation 1)

was 43% higher at NLC than SLC. This was due to faster growth rates at NLC, which had a greater influence on production estimates at the two sites than observed differences in age-specific mortal-ity rates. Model predictions of leaf biomass production were within the range of more direct measurements of cumulative above ground production at other sites in WCA 2A (Davis, 1984, Figure 8B), particularly if Davis' data points are shifted several increments to the right to account for small leaves that were not included in his measurements (Davis, pers. comm.).

Standing crop biomass of shoot bases, rhizomes, and roots of individual live plants provided direct measurements of cumulative production of these plant parts, assuming sloughing of these tissues was minimal. Shoot base and root production were highly correlated with plant growth (i.e., shoot base length) at both sites (Figure 9). Adjusted means of logarithmic relationships between shoot base biomass and shoot base length were significantly higher at SLC (ANCOVA, $p(F) < .001$), while slopes and adjusted means of linear regressions between root biomass and plant growth were significantly higher at NLC (ANCOVA, $p(F) < .001$). Poor correlations between shoot base length and rhizome biomass (Figure 10A), as well as cumulative number of rhizomes (Figure 10B), suggests that factors other than growth stage have a major influence on cattail rhizome production.

Combined shoot base, rhizome and root biomass of individual live plants at SLC was slightly higher (ANCOVA, $p(F) < .001$) than among comparable growth stages at NLC (Figure 11); however, below ground production of cohorts[1] was 32% higher at NLC than at SLC. As with differences in cohort leaf production, this site difference in below ground production was due to faster growth rates and greater survival rates of advanced growth stages at NLC. Below ground plant parts accounted for approximately 24% of total lifetime biomass production of cattail cohorts at each site.

Nutrient Concentrations of Plant Tissues

Because nutrient concentrations in new shoot tissues are diluted as young plants grow (Ulrich, 1952; Smith, 1962; Boyd, 1970a; Prentki et al., 1978; Shaver and Melillo, 1984), divisive cluster analyses[2] were utilized to differentiate young and mature plant growth categories. Based upon these analyses, plants with shoot base lengths ≤ 5.0 cm were interpreted as young plants while plants with shoot base lengths > 5.0 cm were designated mature plants.

Nutrient concentrations of live plant components were significantly different ($p(F \text{ or } t) < 0.05$) between growth categories, sites and sampling dates. Nutrient concentrations of most live plant tissues of young shoots were higher than comparable plant parts in mature culms; nutrient concentrations

(1) Calculated by substituting site-specific below ground production of cattail with shoot base lengths = i for CLP(i) in equation 2.

(2) Separate analyses were conducted on standardized TKN and P concentrations of individual plant components, based upon Euclidean distance between each case and the mean (center) of all cases in the cluster. Nutrient concentrations were standardized (divided by standard deviations) to eliminate bias resulting from difference in scale associated with TKN and P measurements.

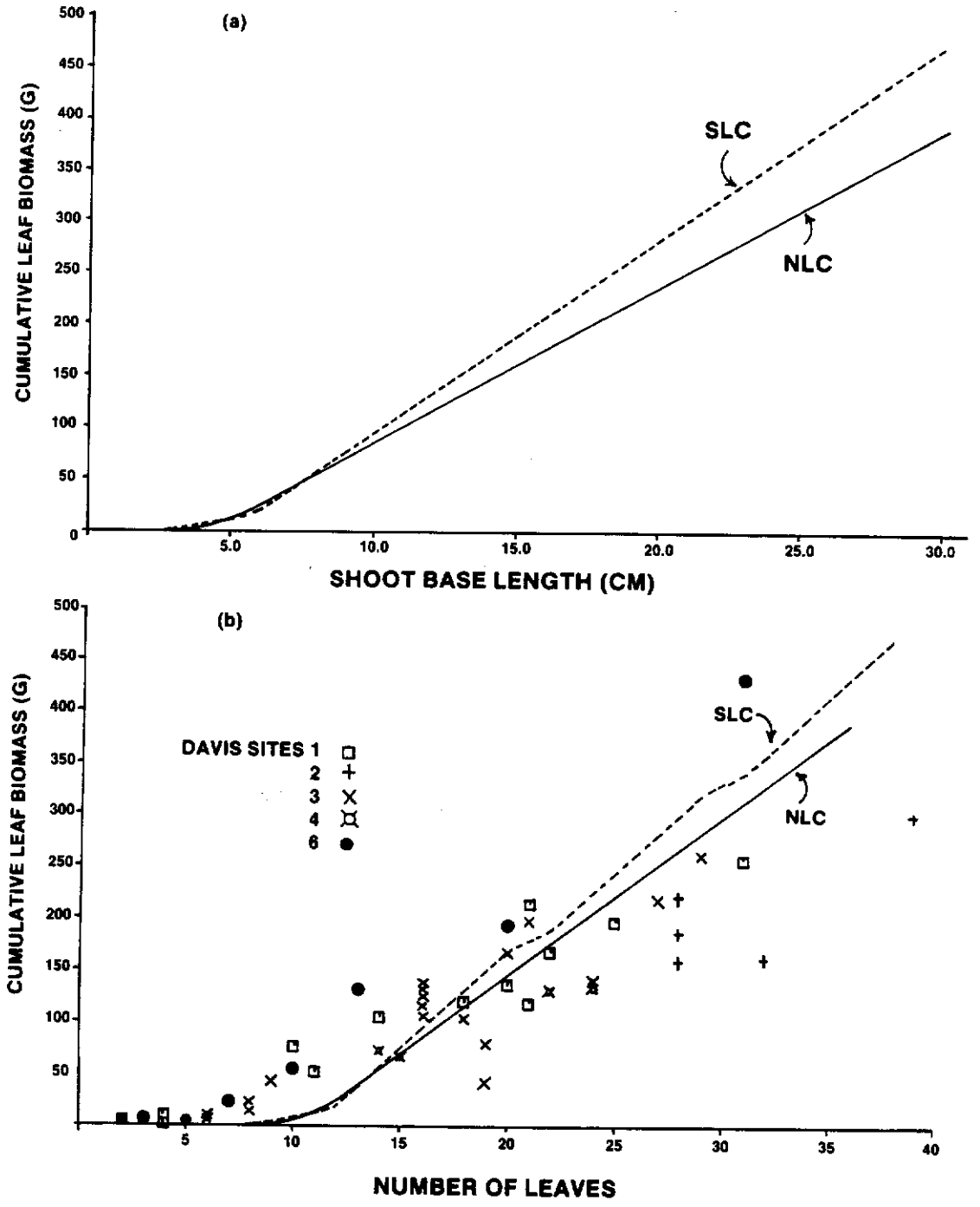

FIGURE 8 Cumulative (Lifetime) Leaf Biomass Production at NLC and SLC Based Upon Equation (1). (a) Relationships Between Lifetime Leaf Biomass Production and Shoot Base Length, (b) Relationships Between Leaf Biomass Production and Cumulative Number of Leaves Produced During Lifetimes of Plants. Davis' (unpubl.) Measurements of Lifetime Leaf Biomass Production at Four Other Locations in Water Conservation Area 2A are Also Shown.

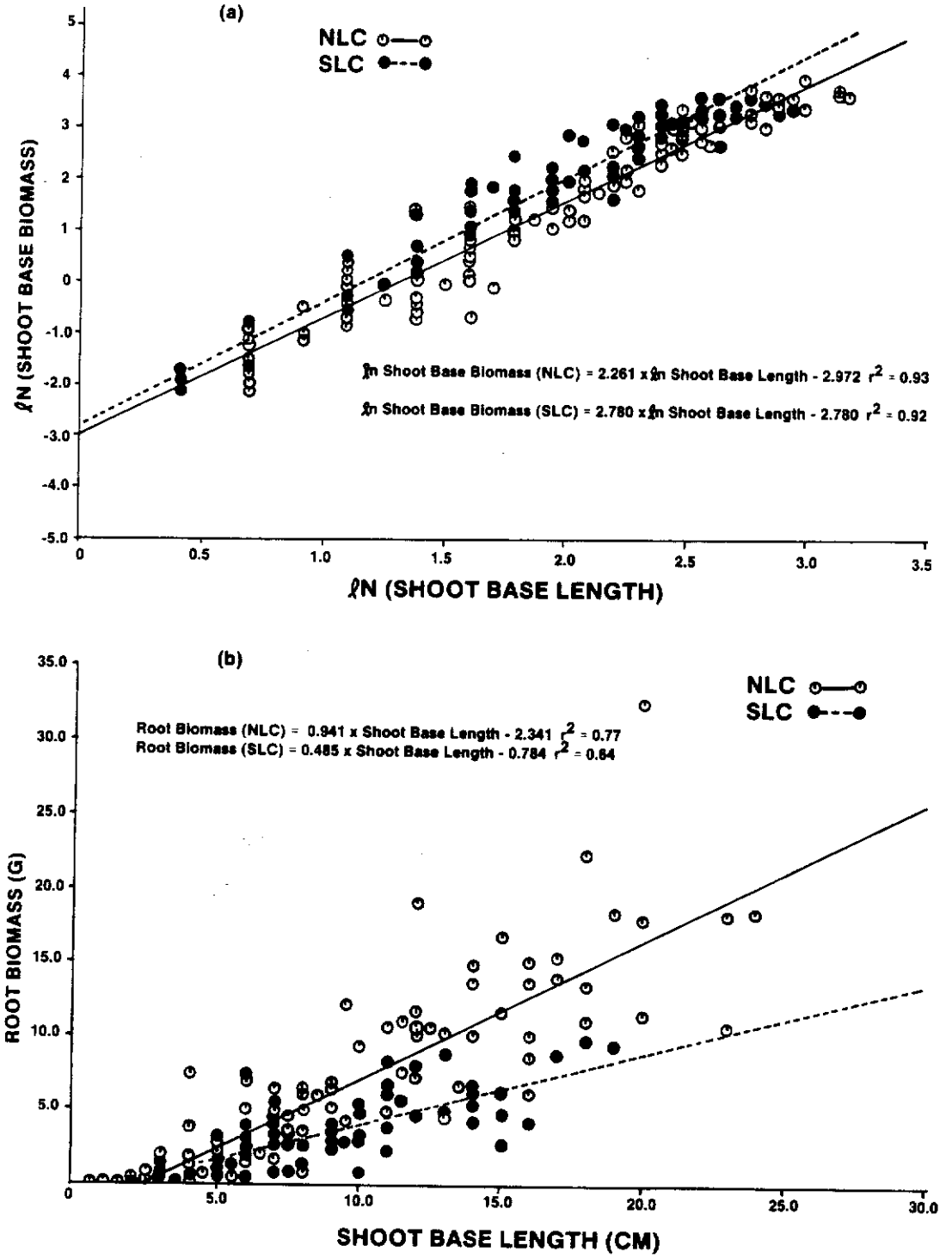

FIGURE 9 Lifetime Shoot Base and Root Biomass Production and NLC and SLC. (a) Log_e - Log_e Relationships Between Cumulative Shoot Base Biomass Production and Shoot Base Length, (b) Linear Relationships Between Cumulative Root Biomass Production and Shoot Base Length.

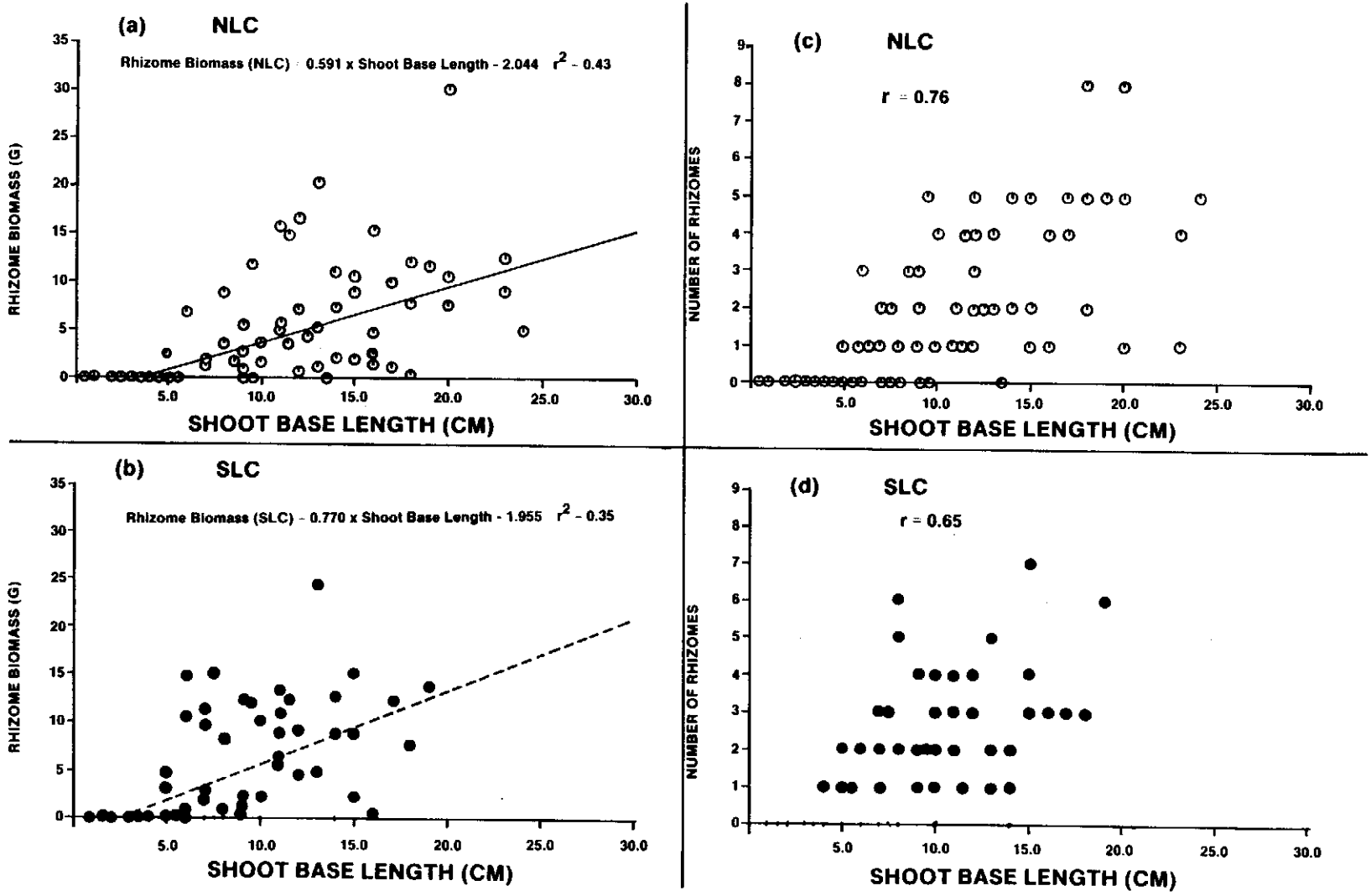

FIGURE 10 Relationships Between Plant Growth (Shoot Base Length) and Cumulative Rhizomone Biomass Production (a,b) and Total Numbers of Rhizomes Produced During Plant Lifetimes (c,d).

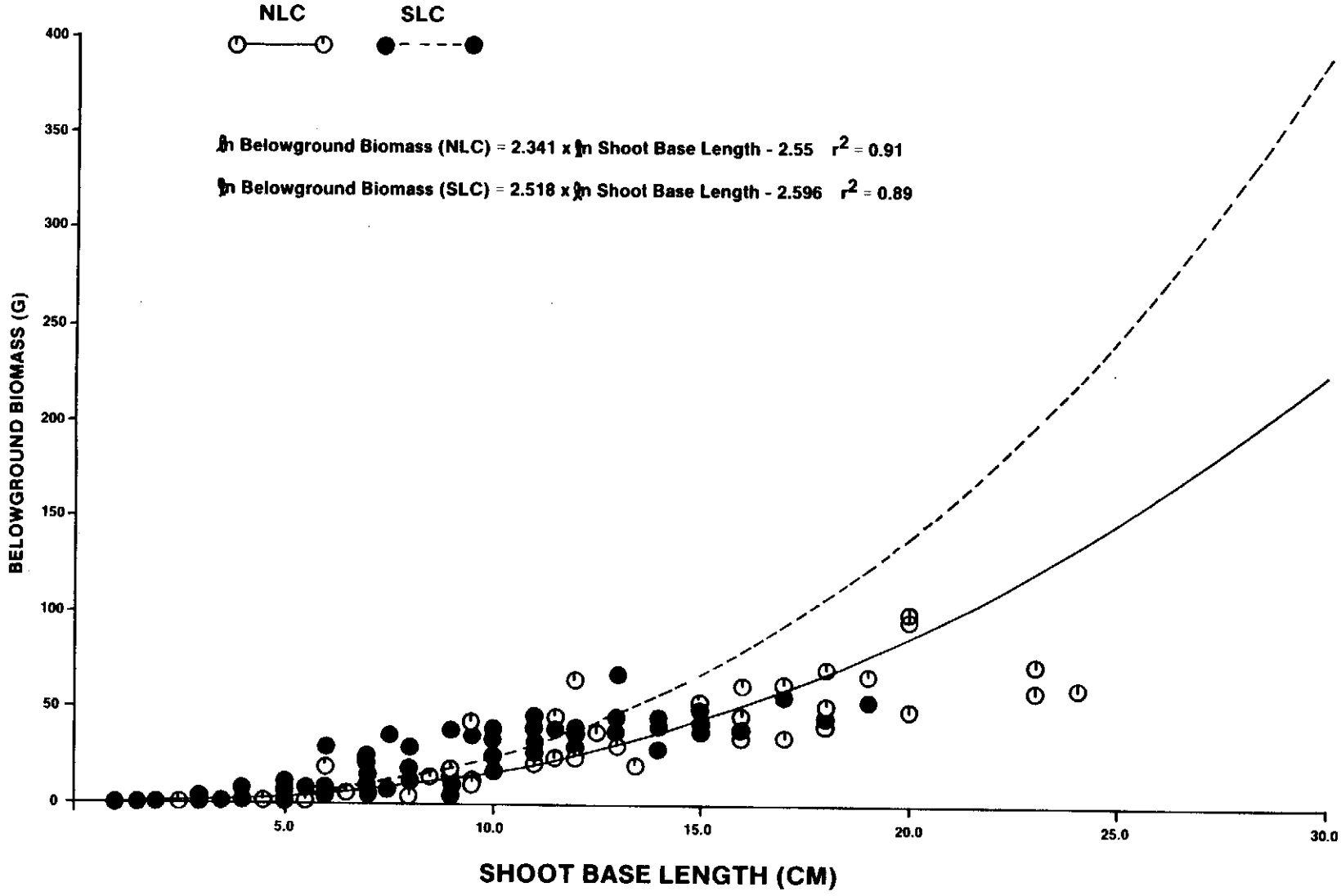

FIGURE 11 Cumulative (Lifetime) Belowground Production in Relation to Shoot Base Lengths at NLC and SLC.

were also higher at NLC than at SLC (Table 3). Highest nitrogen and phosphorus concentrations were typically found in shoot bases, and lowest concentrations occurred in remnant leaves. Differences in nutrient concentrations among plant components were least prominent in mature plants at SLC.

Patterns of variability among sampling dates included declines in nitrogen and phosphorus concentrations of live leaves at both sites during summer and fall (Appendix 1). Nutrient concentrations of below ground plant parts at NLC underwent a similar decline during these sampling periods, whereas TKN and P concentrations of shoot bases, rhizomes and roots of live plants at SLC increased during the summer. Thus, there was some evidence of translocation of nutrients between above ground and below ground plant components at SLC.

Nutrient concentrations of dead and remnant plant components (Table 4) indicate that cattail tissues release substantial amounts of accumulated nitrogen and phosphorus as they die and begin to decompose. Phosphorus concentrations of dead leaves, for example, were 70-79% lower than concentrations found in live leaves, while nitrogen concentrations of dead leaves were 48-55% lower than live leaf tissues. Although below ground components of dying plants typically retained a higher proportion of accumulated nutrients than leaf tissues, phosphorus concentrations in shoot bases of dead plants were as much as 59% lower than in live shoot base tissues. Further declines in nutrient concentrations of remnant plant tissues indicate that nitrogen and phosphorus remaining in dead plant tissues are released more rapidly than the rate of weight loss during initial stages of decomposition. Based upon differences in nutrient concentrations in live and remnant plant tissues, it appears that phosphorus is particularly labile and most readily released from leaf tissues. In contrast, accumulated nitrogen is comparatively stable, especially in roots and rhizomes.

TABLE 3. Mean Nitrogen (TKN) And Phosphorus Concentrations (% Dry Weight) of Live Plant Components. Means were derived from average nutrient concentrations during each sampling period. Except as noted, all nutrient concentrations were significantly different ($p(F \text{ or } t) < 0.05$) between age classes and sites.

NLC

	TKN(%)			P(%)	
	Young		Mature	Young	Mature
Live Leaves	1.46		0.97	0.194	0.100
Dead Leaves	+0.64		0.48	+0.056	0.026
Remnant Leaves	+0.37	*	0.34++	+0.023	0.016
Shoot Bases	2.27		1.11	0.347	0.155
Rhizomes	-		0.60++	-	0.074
Roots	0.84		0.68	0.086	0.057

SLC

	TKN(%)			P(%)	
	Young		Mature	Young	Mature
Live Leaves	1.07		0.71	0.130	0.058
Dead Leaves	+0.55		0.36	+0.041	0.016
Remnant Leaves	+0.39	*	0.39++	+0.018	0.012
Shoot Bases	1.26		0.64	0.129	0.052
Rhizomes	-		0.55++	-	0.057
Roots	0.63	*	0.61	0.046	0.034

* Concentrations were not significantly different (Date X Age ANOVA) between young and mature plants.

\+ TKN and P concentrations of dead and remnant leaves of young plants were not significantly different (t-tests) between sites.

++ TKN concentrations of remnant leaves and rhizomes of mature plants were not significantly different (Date X Site ANOVA) between sites.

TABLE 4. Mean Nitrogen (TKN) and Phosphorus (P) Concentrations (% Dry Weight) of Dead and Remnant Plant Components. Means were derived from mean nutrient concentrations dsuring each sampling period.

NLC

	TKN (%)				P (%)			
	Dead Plants		Remnant Plants		Dead Plants		Remnant Plants	
	Young	Mature	Young	Mature	Young	Mature	Young	Mature
Dead Leaves	0.69	0.46	-	-	0.042	0.021	-	-
Remnant Leaves	0.37	0.36	0.50	0.48	0.023	0.017	0.041	0.020
Shoot Bases	1.41	1.04	0.93	0.57	0.142	0.086	0.120	0.043
Rhizomes	-	0.60	-	0.43	-	0.058	-	0.040
Roots	0.64	0.64	0.65	0.61	0.049	0.038	0.034	0.027

SLC

	TKN (%)				P (%)			
	Dead Plants		Remnant Plants		Dead Plants		Remnant Plants	
	Young	Mature	Young	Mature	Young	Mature	Young	Mature
Dead Leaves	0.62	0.36	-	-	0.035	0.011	-	-
Remnant Leaves	0.50	0.49	0.85	0.72	0.016	0.013	0.023	0.017
Shoot Bases	0.94	0.53	0.72	0.49	0.064	0.031	0.042	0.019
Rhizomes	0.64	0.42	0.47	0.50	0.043	0.034	0.024	0.022
Roots	0.62	0.48	0.66	0.60	0.030	0.019	0.033	0.020

Cumulative Nutrient Uptake and Flux in Plant Tissues

Due to faster growth rates, greater survival of advanced growth stages, and higher tissue nutrient concentrations, live cattail at NLC accumulated more nitrogen and phosphorus than plants at SLC. Based upon growth-production relationships, survivorship curves, and tissue nutrient concentrations, i.e.,

$$\sum_{i=1.0}^{x} S(i) * CLP(i) * LNC(i) \quad (3)$$

where

x = shoot base length

S(i) = survivorship of cattail with shoot base lengths = i

CLP(i) = cumulative leaf production of cattail with shoot base lengths = i

LNC(i) = nitrogen or phosphorus concentration of live leaves of cattail with shoot base lengths = i (from Table 3),

live leaves of cattail cohorts at NLC accumulated 95% more nitrogen and 136% more phosphorus than foliage of cohorts at SLC. Below ground plant components of cohorts at NLC accumulated 87% more nitrogen and 185% more phosphorus than shoot bases, rhizomes and roots at SLC; however, below ground components stored only 20-23% of the total nitrogen and phosphorus accumulated by cattail tissues at each site. Thus, nutrient dynamics associated with leaf production was the dominant uptake pathway during a plant's lifetime and accounted for the greatest portion of site differences in total nutrient accumulation.

Differences in nitrogen and phosphorus concentration between live and dead plant components were used to ascertain cumulative lifetime losses of nutrients that occur during plant death. These losses amounted to 42-43% of total accumulated nitrogen and 69-71% of accumulated phosphorus at the two sites. Leaf tissues accounted for the greatest nutrient losses (Figure 12). Dead leaves retained 48-51% of nitrogen and only 22% of phosphorus accumulated by live leaf tissues of cohorts at each site (Figure 13). Proportional losses by below ground tissues were smaller (Figure 13) and nutrient retention by dead shoot bases, rhizomes and roots represented 17-19% of total nitrogen and 12-14% of total phosphorus accumulated by live plants at the two sites.

DISCUSSION

Population characteristics of cattail at NLC and SLC indicate that selective forces influencing life history patterns differ at these locations in WCA 2A. High mortality of young shoots at NLC is probably due to limited light infiltration through the dense canopy of cattail foliage at this site. In contrast, cattail

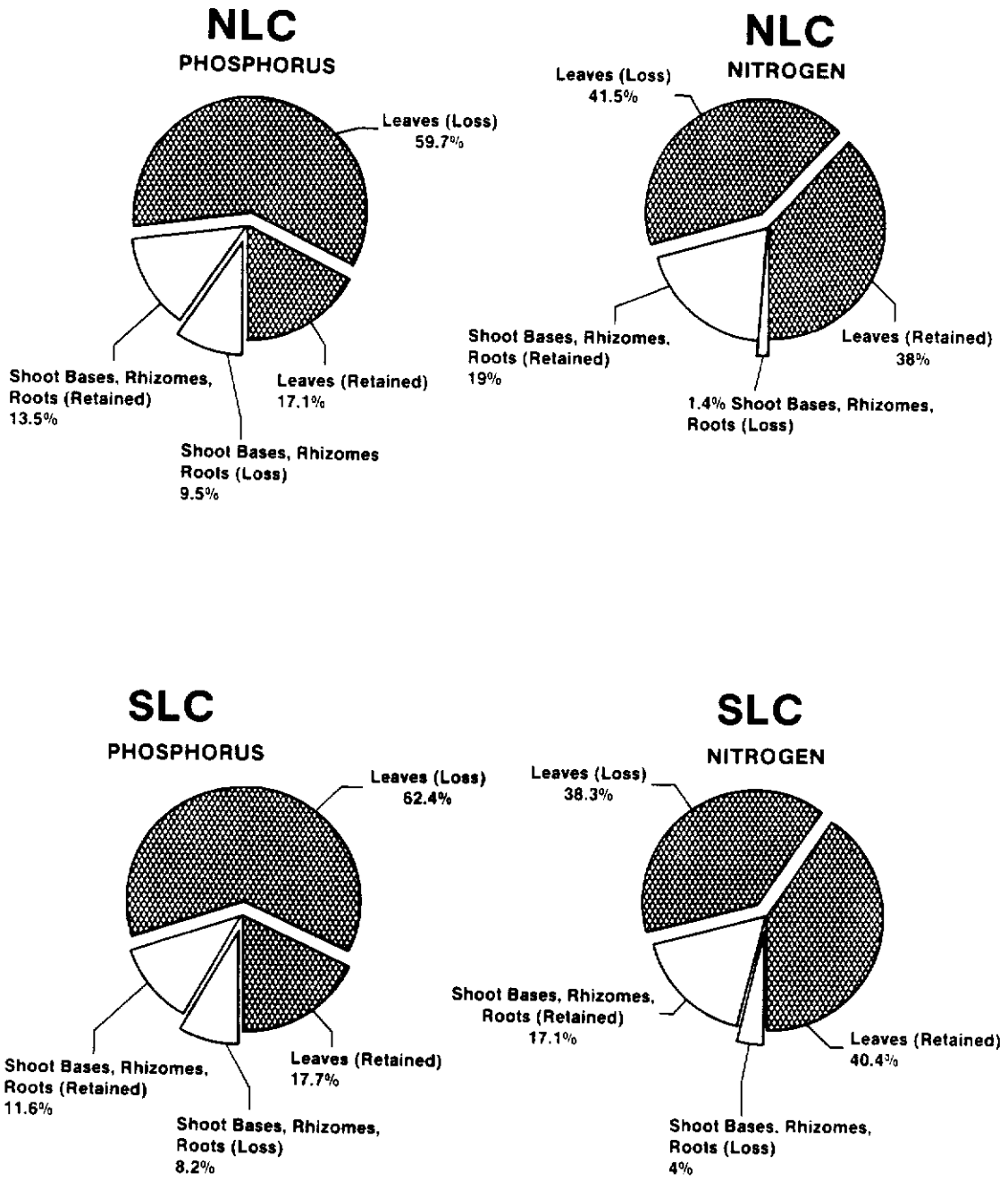

FIGURE 12 Lifetime Nutrient Loss and Retention by Cattail Tissues Relative to Total Nutrient Accumulation by all Plant Components.

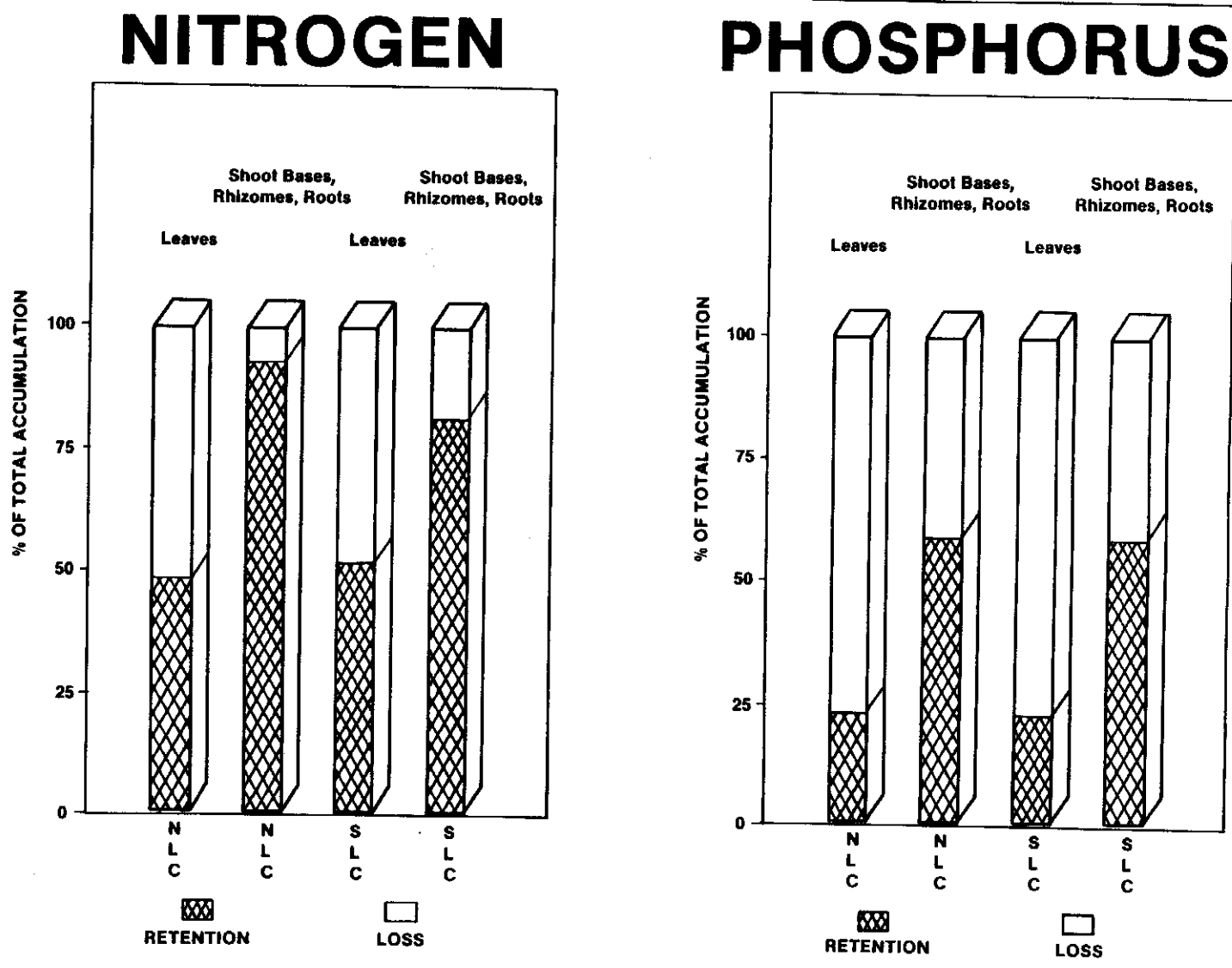

FIGURE 13 Lifetime Nutrient Loss and Retention by Cattail Tissues Relative to Total Nutrient Accumulation by Each Plant Component.

recruitment in SLC sloughs is clearly not restricted by light availability, and expansion into the adjacent sawgrass marsh has been facilitated by gaps in the marsh canopy that result from the tussock growth form which sawgrass has adopted in response to prevailing water level regimes in this area (Toth, 1987).

Hydrologic and climatic conditions appear to be the primary causes of cattail mortality at SLC. Cattail at this site sustained complete above ground mortality when water levels fell below the ground surface as a winter cold front passed through the region in 1985. The relative influence of density-dependent and density-independent forces on cattail mortality schedules at NLC and SLC are similar to effects of these factors on Typha latifolia biotypes from open and shaded habitats (Grace and Wetzel, 1981).

Higher tissue nutrient concentrations, growth rates, and production of surviving plants at NLC relative to cattail at SLC, may be attributable to a relationship between hydrologic conditions and nutrient availability. Because nutrient inputs appear to be similar at NLC and SLC, nutrient availability at these sites is at least partially dependent upon the fate of nutrients released by dead and dying plant tissues, particularly leaf tissues. Stagnant water conditions at NLC promote retention of released nutrients, and thereby foster development of a self-sustaining nutrient recycling pathway which provides a continuous supply of nutrients for new plant growth. At NLC this "external" nutrient recycling path-way appears to maximize cattail leaf production and is constrained only by plant density limitations. In contrast, surface water flows accompanying wide water level fluctuations at SLC, lead to continuous export of nutrients released by decomposition processes. In the absence of an effective external recycling pathway, cattail growth at SLC is facilitated by internal storage and translocation of nutrients from tissues of parent plants to offshoots. Summer translocation of nutrients from above ground to below ground tissues was evident at SLC and may account for high early survivorship at this site despite low nutrient availability. While this internal recycling mechanism can be an effective nutrient conservation strategy for plant reproduction, trans-location rate constraints may permit considerable losses of nutrients via leaching and/or decomposition. Prentki et al. (1978) found that over-winter, below ground reserves contributed about 40% of phosphorus required for above ground growth of T. latifolia offshoots, but annual retention of phosphorus represented only 30% of annual peak storage. Although internal recycling is adaptive in nutrient poor habitats (Boyd, 1971) and seasonal latitudes with short growing seasons (McNaughton, 1974; Fiala, 1978; Prentki et al., 1978), it is likely ineffective in preventing substantial nutrient export from areas with hydrologic conditions like those that occur at SLC.

Differences in rates and locations at which nutrients are released from dead plant tissues may lead to other pathways of nutrient flux. Although a high rate of nutrient release from dead leaf tissues (Boyd, 1970b; Mason and Bryant, 1975; Purvieth, 1980; Davis, 1984; this study) appears to facilitate high rates of external nutrient recycling at NLC and nutrient export at SLC, results of this study suggest that the fate of accumulated nitrogen differs from that of accumulated phosphorus. Leaf tissue concentrations and soil nutrient depth distribution data indicate that a larger percentage of accumulated nitrogen is retained and stored in the soil complex. Nitrogen content of dead cattail leaves is more stable than phosphorus content of dead leaves, and continuous deposition of leaf litter appears to lead to burial of incorporated nitrogen below the soil surface, where decomposition processes and further nutrient release occur at a much slower rate (Hackney and de la Cruz, 1980). Rates of nitrogen and phosphorus release from dead shoot bases, rhizomes and roots suggest that a proportion of nutrients accumulated by below ground plant components are also trapped in the soil. Assuming nutrients released by decomposition of dead below ground tissues do not undergo further uptake, shoot bases, rhizomes and roots deposit a maximum of 17-19% of total nitrogen and 12-14% of phosphorus accumulated by cattail cohorts at NLC and SLC. Hence, burial of dead plant tissues is an additional pathway of nutrient flux and a potentially significant means by which cattail may act as a permanent nutrient sink.

Population characteristics of cattail at NLC and SLC are similar in several respects to those of sawgrass at these locations in WCA 2A (Toth, 1987). As with cattail, sawgrass biomass production is higher at NLC due to faster growth rates and a greater frequency of more advanced growth stages at this site relative to SLC. Nutrient dynamics associated with leaf production and turnover constitute the dominant nutrient accumulation pathway for both sawgrass and cattail, and below ground tissues retain a similar percentage of total lifetime nutrient accumulation by each species. Nutrient concentrations of comparable sawgrass and cattail tissues are also similar, and reflect higher nutrient availability at NLC. Production and nutrient dynamics of both species conform to differences in nutrient recycling pathways at the two locations.

While these characteristics suggest that sawgrass and cattail respond similarly to hydrologic conditions at NLC and SLC, water level regimes appear to impact sawgrass more than cattail. In addition to effects on sawgrass growth rates, hydrologic conditions influence sawgrass mortality schedules, growth form and life history strategies. Tussock formation, slow growth rates, and heavy early mortality coupled with high rates of new shoot production are all characteristics of sawgrass subjected to stresses associated with deep and widely fluctuating water levels. Moreover, shorter leaf growth, and hence, lower leaf production by sawgrass at SLC relative to comparable growth stages at NLC can be tied to the relationship between hydrologic conditions and nutrient availability at the two sites. In contrast, although the hydrologic regime is a primary contributor to above ground cattail mortality at SLC, growth forms and new shoot production of NLC and SLC cattail are similar, and there are no major differences in leaf height/production of comparable growth stages at the two sites.

Results of this study suggest that cattail expansion in WCA 2A is mediated by an interaction between hydrologic conditions and nutrient availability. Cattail is an extremely opportunistic species that is capable of a rapid rate of expansion (Fiala, 1971) in a wide range of environmental conditions. However, at SLC nutrients are limited and combined effects of seasonally low water levels and winter cold fronts temporally restricts the cattail growing season. In these conditions cattail life history strategies must provide for adequate below ground energy reserves for survival during winter, and a sufficient supply of nutrients in below ground tissues for new growth during the subsequent growing season. Since the ability of cattail to acquire large below ground stores of energy and nutrients is severely limited by low nutrient availability at SLC, rapid cattail expansion in this section of WCA 2A does not appear to be imminent. In contrast, in addition to providing favorable water levels for an extended growing season, hydrologic conditions at NLC promote development of an external recycling pathway that maintains a continuous supply of nutrients for plant growth. Although cattail and sawgrass exhibit similar lifetime production responses to prevailing hydrologic/nutrient regimes at NLC, cattail appears to have a competitive advantage due to greater annual production (Davis, 1988) and a faster rate of vegetative spreading. Thus, cattail may continue to replace sawgrass in areas with hydrologic regimes that are comparable to conditions at NLC.

CONCLUSIONS

1. Lifetime biomass production and associated nutrient uptake are greater where cattail grows in shallow, stagnant water than in stands subjected to water regimes that are predominantly deep and undergo unnaturally wide fluctuations. Results suggest that long-term detention of surface water leads to maximum nutrient uptake in Everglades habitats with low nutrient inputs.

2. Nutrient flux associated with leaf production dominates lifetime nutrient dynamics of cattail and is of overriding importance in evaluations of the nutrient storage potential of this species. Belowground plant parts permanently retain a maximum of 17-19% of total nitrogen and 12-14% of total phosphorus accumulated by typical cattail cohorts.

3. Deep and unnaturally fluctuating water level regimes adversely impact sawgrass more than cattail.

RECOMMENDATIONS

Results of this study should be integrated with other Environmental Sciences Division research dealing with ecological implications of current and proposed water management options and practices.

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APPENDIX 1. NITROGEN AND PHOSPHORUS CONCENTRATIONS (% DRY WEIGHT) OF LIVE PLANT COMPONENTS DURING EACH SAMPLING PERIOD.

	Winter 84	Spring 84	Summer 84	Fall 84	Winter 85
		TKN Concentrations - Young Plants (NLC)			
Live Leaves	1.63	1.27	1.85	1.30	1.38
Dead Leaves	0.55	0.64	0.57	0.76	0.69
Remnant Leaves	0.39	0.35	-----	0.43	0.31
Shoot Bases	2.31	2.63	1.85	2.40	1.76
Roots	0.86	0.88	0.79	0.69	0.85
		TKN Concentrations - Mature Plants (NLC)			
Live Leaves	1.15	1.05	0.86	0.78	1.10
Dead Leaves	0.49	0.59	0.43	0.39	0.51
Remnant Leaves	0.42	0.37	0.33	0.34	0.28
Shoot Bases	1.38	1.66	1.09	0.77	0.78
Rhizomes	0.64	0.67	0.58	0.54	0.59
Roots	0.72	0.86	0.60	0.62	0.62
		P Concentrations - Young Plants (NLC)			
Live Leaves	0.217	0.147	0.309	0.198	0.165
Dead Leaves	0.050	0.039	0.091	0.065	0.086
Remnant Leaves	0.029	0.013	------	0.025	0.021
Shoot Bases	0.348	0.373	0.263	0.336	0.343
Roots	0.096	0.076	0.101	0.068	0.093
		P Concentrations - Mature Plants (NLC)			
Live Leaves	0.114	0.100	0.089	0.076	0.129
Dead Leaves	0.026	0.031	0.023	0.019	0.030
Remnant Leaves	0.022	0.015	0.018	0.015	0.012
Shoot Bases	0.163	0.231	0.164	0.103	0.122
Rhizomes	0.075	0.090	0.091	0.066	0.059
Roots	0.065	0.072	0.051	0.051	0.052
		TKN Concentrations - Young Plants (SLC)			
Live Leaves	1.22	0.99	0.66	0.98	1.55
Dead Leaves	0.41	0.50	0.34	0.65	0.89
Remnant Leaves	0.36	0.33	0.40	0.49	-----
Shoot Bases	1.29	1.02	1.23	2.22	1.17
Roots	0.67	0.60	0.61	1.06	0.49
		TKN Concentrations - Mature Plants (SLC)			
Live Leaves	0.91	0.82	0.53	0.54	1.58
Dead Leaves	0.38	0.35	0.36	0.29	0.68
Remnant Leaves	0.41	0.39	0.38	0.40	-----
Shoot Bases	0.67	0.57	0.69	0.57	0.57
Rhizomes	0.57	0.45	0.61	0.57	0.43
Roots	0.58	0.59	0.64	0.68	0.47
		P Concentrations - Young Plants (SLC)			
Live Leaves	0.137	0.117	0.068	0.140	0.217
Dead Leaves	0.023	0.050	0.022	0.054	0.053
Remnant Leaves	0.024	0.009	0.017	0.021	-----
Shoot Bases	0.109	0.120	0.132	0.317	0.079
Roots	0.054	0.052	0.033	0.073	0.023
		P Concentrations - Mature Plants (SLC)			
Live Leaves	0.071	0.063	0.048	0.043	0.194
Dead Leaves	0.016	0.013	0.018	0.011	0.039
Remnant Leaves	0.015	0.011	0.012	0.009	-----
Shoot Bases	0.051	0.042	0.063	0.042	0.044
Rhizomes	0.059	0.043	0.072	0.057	0.035
Roots	0.036	0.030	0.035	0.036	0.023